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The significance of optical properties in competition among visual and tactile planktivores: a theoretical study

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Abstract

A mathematical model describing competition for a common food resource among visual and tactile planktivores is developed. Sensitivity of the competitive regime to environmental changes are studied by analysing their effects on foraging rates and niche availability of both planktivore types. Depth, spatial, daily and seasonal variations in factors of biotic and abiotic origin may result in great changes in the competitive regime. Optical properties of the water column is of greatest importance for competition. In addition the abundance and size of prey, small scale turbulence, and the seasonal and daily variations in sun irradiance are of importance. Inherent contrast of prey organisms is likely to modify the effect from the above factors under certain circumstances only, but may together with prey size, also enhance niche differentiation among the competitors. By studying the zero growth rate isoclines for populations of tactile and visual planktivores at different depths, we show that the water column is a habitat divided into different competitive regimes. These can be thought of as relatively stable niches separated by an ecotone of rather unpredictable and ever changing competitive regime, due to changes in environmental factors. In most cases it is optimal for visual planktivores to stay at shallow depths, while tactile planktivores compete better at greater depths. However, by simulations we show that high predation pressure can make near surface waters hostile to many visual planktivores such as fish, thereby making this highly productive niche available to tactile planktivores such as jellyfish. Results are discussed in relation to naturally occurring environmental variations and the impact of anthropogenic factors. Changes in optical properties due to eutrophication might have drastic effects on the outcome of competition, and thus on the structure of marine food chains. While too little is known about the physiology, life history and behaviour of most pelagic organisms to make specific predictions, this work indicates a potential for strong competitive interactions among different functional types of planktivores. © 1997 Elsevier Science B.V.

Keywords: Visual planktivores; Tactile planktivores; Competition; Water optics

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1. Introduction

Rather rapid changes in the composition of planktonic communities are known from the literature. Often these reports refer to mass appearances of gelatinous zooplankton lasting from months to decades. For instance mass abundances of the scyphozoa *Pelagia noctiluca* are known from the Mediterranean Sea (Legovic, 1987; Goy et al., 1989; Axiak et al., 1991), the scyphozoa *Aurelia aurita* in the Baltic sea (Möller, 1980a,c) and in the Black Sea together with the ctenophore *Mnemiopsis leidyi* (Zaitsev, 1992), and the scyphozoa *Periphylla periphylla* in a Norwegian fjord (Fosså, 1992). Typically these mass occurrences are believed to be caused by environmental changes such as abnormal winter temperature (Legovic, 1987), wind and current aggregations (Goy et al., 1989, Axiak et al., 1991), or anthropogenic impact (Zaitsev, 1992).

It has been suggested that large abundances of gelatinous zooplankton might affect other organisms, especially fish, both as predators (Möller, 1979; 1984) and as competitors for a common food resource (Fraser, 1970; Möller, 1980b; Allredge, 1984). Zaitsev (1992) claims that the number of commercially harvested fish species in the Black Sea has declined dramatically after the increase in abundances of *A. aurita* and *M. leidyi*. Likewise, *P. periphylla* is reported to have appeared in vast numbers in a Norwegian fjord since the 1940s, possibly due to the exclusion of pelagic fish such as *Maurolicus muelleri* and *Benthoosema glaciale*, abundant in nearby fjords (Fosså, 1992).

While most fish rely on visual sensing of their prey, the gelatinous organisms depend on physical contact with prey on certain specialised surfaces. Thus, while the efficiency of fish predation depends on light availability, the tactile predation efficiency does not. Light availability is therefore crucial and by means of a model of the instantaneous visual and tactile predation, represented by traits common to fish and jellyfish, we investigate how properties of the pelagic environmental regime might affect the competition between tactile and visual planktivores.

2. The model

Over time, competition will eventually affect the performance of populations which may be measured by the instantaneous rate of population increase (r). Unfortunately, neither the performance of a population, nor changes in this parameter brought about by environmental unsuitability, can easily be computed. Therefore, effects of competition must be sought in secondary performance estimates.

Based on the Lotka-Volterra equation (Lotka, 1925; Volterra, 1926), we define a depth and time specific measure of habitat profitability ($H(Z, t)$) as the expected instantaneous contribution to the reproductive rate of an individual:

$$H_1(Z, t) = r_1 \cdot \frac{K_{C1}(Z, t) - N_1(Z, t) - \alpha_{12}(Z, t) \cdot N_2(Z, t)}{K_{C1}(Z, t)} \quad (1a)$$

where $K_{C1}(Z, t)$ is depth (Z) and time (t) specific carrying capacity, r_1 denotes the average potential instantaneous rate of increase in absence of competition for a population N_1 individual and $\alpha_{12}(Z, t)$ describes the effects of a competing population N_2 . The distribution of the two populations ($N_1(Z, t)$ and $N_2(Z, t)$), and of the carrying capacity ($K_C(Z, t)$ if interpreted as the distribution of food) is determined by a game between two competing predators and a common prey. This is not considered in the present work. Instead we focus on the competition coefficient ($\alpha_{12}(Z, t)$) which, we shall argue, is determined by the physical properties of the habitat independently of population dynamics. Therefore, we will treat all factors except α as constants, in order to study the objective (i.e. environmentally constrained) aspect of habitat profitability:

$$H_1(Z, t) = r_1 \cdot \frac{K_{C1} - N_1 - \alpha_{12}(Z, t) \cdot N_2}{K_{C1}} \quad (1b)$$

Later we will discuss how this coefficient may vary in space and time.

2.1. Measures of competition

2.1.1. Lotka-Volterra approach

In exploitative competition, α_{12} represents the rate of resource removal of an individual of species 2 measured in terms of species 1 equivalents. For the simplest exploitative competition $\alpha_{12} = (\alpha_{21})^{-1}$. For pelagic planktivores, environmental variability of potential influence on the food intake rate, are strong in the vertical axis. At depth Z and time t , the relative performance of visual and tactile competition may be denoted by

$$\alpha(Z, t) = \frac{i_V(Z, t)}{i_T(Z, t)} \quad (2)$$

where $i_V(Z, t)$ and $i_T(Z, t)$ are depth and time specific ingestion rates for the visual and the tactile planktivore respectively (Table 1). Let N_1 of Eq. (1b) denote a population of tactile planktivores and N_2 denote a visual planktivore population. Then $\alpha(Z, t)$ corresponds to α_{12} at depth Z , and $\alpha(Z, t)^{-1}$ corresponds to the α_{21} coefficient. $\alpha(Z, t) < 1$ indicates that tactile predation is more efficient, while $\alpha(Z, t) > 1$ indicates that visual predation is most efficient.

2.1.2. Equilibrium depth approach

If the two feeding strategies are equally efficient in terms of individual prey removal, at a particular depth, this depth is termed the equilibrium depth (Z_{EQ}):

$$\frac{f_V(Z_{EQ})}{f_T(Z_{EQ})} = 1 \Leftrightarrow f_V(Z_{EQ}) = f_T(Z_{EQ}) \quad (3)$$

where f_V and f_T denotes handling and encounter restricted foraging rates of visual and tactile planktivores, respectively (Table 1). Observe that in contrast to i, f is not restricted by gut capacity and therefore obtainable over short periods of time only. We use f here simply to avoid the difficulties associated with using the i function (Eq. (12)).

2.2. Habitat profitability

While Eqs. (2) and (3) shows the relative power of the two competitors, the risk of predation must be included to assess the habitat profitability. The

effect of predation can be modelled by subtracting the loss from predation in (Eqs. (1a) and (1b)):

$$H_1(Z, t) = r_1 \cdot \frac{K_{C1} - N_1 - \alpha_{12}(Z, t) \cdot N_2}{K_{C1}} - d_1(Z, t) \quad (4)$$

This equation enables simulations of habitat profitability as a function of depth and time specific competition (K_{C1} , $\alpha_{12}(Z, t)$) and predation risk ($d(Z, t)$) (Table 1). Note that predation will be the only source of mortality considered in our analysis.

2.3. Prey encounter

2.3.1. Tactile predation

In tactile foraging prey encounter is assumed to take place in a circular tactile area situated perpendicularly to the swimming direction of the predator.

Based on studies of *A. aurita* preying upon larval herring (*Clupea harengus*) the individual tactile predation rate (f_T) has been expressed in terms of handling time (h) and encounter rate (e) (Table 1) (Bailey and Batty, 1983):

$$f_T = e \cdot (1 + e \cdot h)^{-1} \quad (5a)$$

Many tactile planktivores are assumed to follow a linear functional response curve over a large spectrum of prey abundances (Alldredge, 1984). This is achieved when handling time in Eq. (5a) approaches zero:

$$\lim_{h \rightarrow 0} f_T = e \quad (5b)$$

The encounter rate between the planktivore and its prey (e) is a function of the velocity component (A) between the two (Eq. (13)), the encounter area (assumed spherical) of the planktivore (πE_T^2) and the prey density ($P(Z)$):

$$e = \pi \cdot E_T^2 \cdot A \cdot P(Z) \quad (6)$$

(see Table 1). If Z denotes depth, and $f_T(Z)$ is predation rate at depth Z , then from the above equations it follows that:

$$f_T(Z) = \pi \cdot E_T^2 \cdot A \cdot P(Z) \quad (7)$$

Table 1
Variables used in Eqs. (1a), (1b)–(5) and (5b)–(16)

Symbol	Description	Value	Unit	Source
β	Radius of prey organisms	0.001	m	Brodskii (1967)
θ	Visual reaction field half angle	30.0	degrees.	Luecke and O'Brien (1981)
ρ	Amount light lost at sea surface	0.5		Sathyendranath and Platt (1989)
δ	Gut evacuation rate		gC/s	
κ	Digestion rate	0.0002	gC/s	Windell and Foltz (1978)
ε	Turbulent kinetic energy dissipation rate		W/m ³	
$\alpha(Z, t)$	Competition coefficient, (depth/time specific)			
ΔS_c	Sensitivity threshold of eye	0.00007	$\mu\text{mol}/\text{m}^2/\text{s}$	Aksnes and Giske (1993)
a	Area of prey ($\pi\beta^2$)		m ²	
A	Combined velocity component		m/s	
b	Birth rate		s ⁻¹	
c	Beam attenuation coefficient	0.4	m ⁻¹	Rosland and Giske (1994)
C	Carbon content of organism		gC/ind	
C_0	Inherent contrast of prey	0.5		Eggers (1977)
$d(Z, t)$	Mortality rate, (depth/time specific)		s ⁻¹	
e	Individual encounter rate		ind/s	
E_0	Irradiance at sea surface	500	$\mu\text{mol}/\text{m}^2/\text{s}$	Sathyendranath and Platt (1989)
E_r	Encounter radius of tactile planktivore	0.06	m	
$f(Z)$	Foraging rate		s ⁻¹	
h	Handling time		s	
$H(Z, t)$	Habitat profitability, (depth/time specific)		gC m ³	
$i(Z, t)$	Ingestion rate, (depth/time specific)		s ⁻¹	
$K_c(Z, t)$	Carrying capacity, (depth/time specific)		ind	
K	Diffuse light attenuation coefficient	0.1	m ⁻¹	Rosland and Giske (1994)
$N(Z, t)$	Population size, (depth/time specific)		ind	
P	Prey abundance	1000	ind/m ³	
$P(Z)$	Depth specific prey abundance		ind/m ³	
r	Instantaneous rate of population growth		s ⁻¹	
R	Reaction distance of visual planktivore		m	
s	Prey separation distance	0.1	m	
sc	Maximum stomach content		gC	
t	Time		s	
T	Subscript denoting tactile planktivore			
u	Swimming speed of prey	0.001	m/s	
v	Swimming speed of planktivore		m/s	
V	Subscript denoting visual planktivore			
w	Turbulent velocity of water	0.02	m/s	
Z	Depth		m	
Z_{EQ}	Equilibrium depth		m	

The values given are used in the basic run.

2.3.2. Visual predation

Under the assumption that the reaction field of a visual planktivore can be treated as a disc shaped area perpendicular to the swimming direction, the reaction field (or encounter sphere) is governed by the angle of the visual field and the visual range of the planktivore. The foraging rate

of a visual planktivore is then given by the product of the reaction field, a velocity component and prey abundance. Visual based feeding rates are assumed to follow the Holling type II functional response.

The visual range is of vital importance to the efficiency of a visual planktivore. It is determined

by ambient light, features of the organisms in question (such as size and contrast), and the optical properties of the water column (scattering and absorption). For simplicity, we assume the optical properties of the water column to be constant with depth.

Aksnes and Giske (1993) give a mechanistic model for visual predation in the pelagic environment, describing the visual range (R) in terms of light flux at the sea surface (E_0), depth (Z), diffuse light attenuation (K), beam attenuation (c), inherent contrast of the prey (C_0) and sensitivity threshold of the eye (ΔS_e) (Table 1).

$$R_2 \cdot e^{cR + KZ} = \rho \cdot E_0 \cdot |C_0| \cdot a \cdot \Delta S_e^{-1} \quad (8)$$

where ρ is the fraction of irradiance lost through the air sea interface and a is the area of the prey item (Table 1). Eq. (8) can be solved for R by Newton-Raphson iteration. Aksnes and Giske (1993) also show R can be fairly well approximated if $Z \gg R$ by:

$$R^2 \approx \rho \cdot E_0 \cdot e^{-KZ} \cdot |C_0| \cdot a \cdot \Delta S_e^{-1} \quad (9)$$

Furthermore, they give a model describing the encounter and handling restricted foraging rate of a visual planktivore (f), which by inclusion of combined relative velocity (Eq. (13)), and depth dependency gives:

$$f_v(Z) = (h + (\pi \cdot (R \cdot \sin \theta)^2 \cdot A \cdot P(Z))^{-1})^{-1} \quad (10)$$

where h is handling time and θ is the reaction field half angle (Table 1).

2.3.3. Gut limitation

Feeding might be restricted by gut evacuation, as a full gut prevents further feeding. With a full gut, the gut evacuation rate (δ) is expressed by:

$$\delta = s_c \cdot \kappa \quad (11)$$

where: s_c is the maximum stomach content and κ is the digestion rate (Table 1). Assuming the planktivore stops feeding once its stomach is full, encounter, handling or gut restricted ingestion (i) is:

$$i = \min(\delta, f(Z)) \quad (12)$$

where $f(Z)$ is given by Eq. (7) (tactile predation) and Eq. (10) (visual predation).

2.3.4. Velocity component and inclusion of water movement in the model

The velocity component of encounter between planktonic organisms is determined by the velocities of the planktivore (v), the prey (u) and the small-scale turbulence, given as the mean square turbulent velocity (w^2) (Rothschild and Osborn, 1988). The velocity component (A) can be described as:

$$A = \frac{(u^2 + 3v^2 + 4w^2)}{3(v^2 + w^2)^{1/2}} \text{ for } v > u$$

$$A = \frac{(v^2 + 3u^2 + 4w^2)}{3(u^2 + w^2)^{1/2}} \text{ for } u > v \quad (13)$$

(Gerritsen and Stricker, 1977; Rothschild and Osborn, 1988).

Under the assumption that turbulence is isotropic and homogenous, the turbulent mean square velocity (w^2) may be approximated by:

$$w^2 = 3.62(\epsilon s)^{2/3} \quad (14)$$

(Rothschild and Osborn, 1988), where ϵ is the rate of turbulent kinetic energy dissipation and s is the separation distance between the objects of interest (Table 1). The average distance between prey organisms (s) in 3 dimensions is: $s = P^{-1/3}$ (Sundby and Fossum, 1990), where P denotes the prey abundance.

2.4. Depth of competitive equilibrium

Equilibrium depth (Z_{EQ}) was earlier defined as the depth where visual and tactile predation are equally effective. This can be computed by substituting Eqs. (7) and (10) into Eq. (3), using the approximation for visual range (Eq. (9)). For simplicity we make the following substitutions:

$$B = h \cdot \pi \cdot \sin^2 \theta \cdot A \quad C = \rho \cdot E_0 \cdot |C_0| \cdot a \cdot \Delta S_e^{-1} \quad (15)$$

then the equilibrium depth is:

$$Z_{EQ} = \ln((P \cdot f_T(Z))^{-1} \cdot T^{-1} - P) \cdot B \cdot C \cdot K^{-1} \quad (16)$$

Table 2

The parameter values of the basic run and variation span of parameters from general and specified model runs together with the source of parameter values and their units (subscripts *P*, *T* and *V* denotes values for prey, tactile and visual planktivores respectively on parameters)

Coefficient	Value/variation span	Unit:	Source:
<i>P</i>	500–2000	ind/m ³	Giske et al. (1990)
<i>K</i>	0.05–0.20	m ⁻¹	Giske et al. (1990); Rosland and Giske (1994)
<i>c</i>	0.20–0.80	m ⁻¹	Rosland and Giske (1994)
<i>β</i>	0.0005–0.0020	m	Brodskii (1967)
<i>C</i> ₀	0.25–1.00	—	Eggers (1977)
<i>E</i> ₀	250–1000	μmol/m ² /s	Sathyendranath and Platt (1989)
<i>w</i> ²	0.00025–0.0010	m ² /s ²	
<i>v</i> _T	0.01	m/s	Berstad pers. com.
<i>v</i> _V	0.04	m/s	Giske et al. (1990)
<i>C</i> _P	0.001–0.06	mgC/ind	Tande (1982)
<i>C</i> _T	44	mgC/ind	Schneider (1988)
<i>C</i> _V	60	mgC/ind	Giske et al. (1990)
<i>s</i> _{CT}	7.0	mgC	Jobling (1981); Båmstedt et al. (1994)
<i>s</i> _{CV}	4.0	mgC	Tande (1982)
<i>Day</i>	1 July		

See Table 1 for details.

2.5. Simulations

A FORTRAN 77 code was developed for simulation studies (Eiane, 1995). Simulations were made for depths down to 300 m. The present parameter setting suggests negligible possibilities for visual predation below this depth. Parameter values were chosen from the literature (Table 2).

One environmental parameter was varied over what we believe to be a naturally occurring variation span at a time. The others were held at the basic run values (Table 2). The sensitivity of the two competition indices ($\alpha(Z, t)$ and Z_{EQ}) to environmental variations were analysed (Jørgensen, 1986). This analysis is concerned with the relative deviations from the basic run in a selected state variable ($\Delta X = X - X_{br}$), given by the current variation in the parameter examined ($\Delta Q = Q - Q_{br}$). The sensitivity of variable X to a variation in parameter Q is then given by:

$$S_x = \frac{\frac{\Delta X}{X}}{\frac{\Delta Q}{Q}} \quad (17)$$

In an earlier version of the model (Eiane, 1995) there is also incorporated a competition measure

based on individual growth rates potentially obtainable under various competitive regimes. Analysis of competition based on this measure gave results similar to the ones obtained by the Lotka-Volterra approach described above and were therefore omitted in the present paper. However, these growth rates were used in the simulations of habitat profitability ($H(Z, t)$) for populations of tactile and visual planktivores under predation pressure (Eq. (4)). Since gelatinous zooplankton tissue has a low energy to volume relationship (Alldredge, 1984; Schneider, 1988), and since there exist little evidence in the literature that these creatures are represented in the diet of dominating higher order predators (but see Fraser, 1970), we assume the predation pressure to be strongest on the visual planktivores.

Depth specific predation pressure upon the planktivores was calculated (Eq. (10)), but with parameter values designed to fit a higher order predator (a larger fish) preying on the tactile and visual planktivores. Simulations of the habitat profitability for visual and tactile planktivores were made for both night and day situations, with both situations of 12 h duration. In addition to simulations of different light regimes this made it possible to simulate a situation of diel vertical

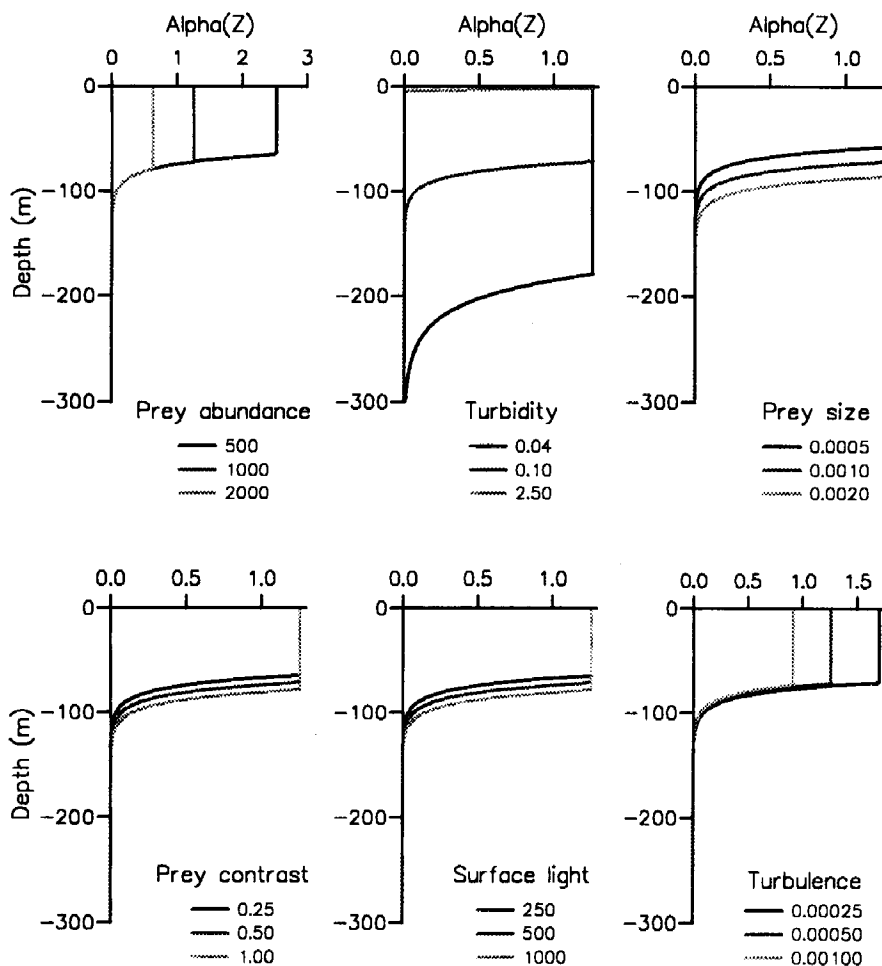


Fig. 1. Competition coefficients ($\alpha(Z, t)$) from model runs where environment coefficients: prey abundance (P), light attenuation (K and c), size of prey organisms (β), inherent contrast of prey (C_0), maximum surface light over day (E_0) and turbulence (w^2), are varied. $\alpha(Z, t)$ for three values of every coefficient are shown.

migrations of the prey. In this study the maximum prey abundance (ca. 1000 ind/m³) is assumed to be normally distributed around a depth of 10 m at night and 100 m at day. The prey abundance, however, was never below 100 ind/m³.

3. Results

At shallow depths $\alpha(Z, t) > 1$ indicates the competitive superiority of visual planktivores (Fig. 1). Here feeding (and then $\alpha(Z, t)$) typically is constant due to gut limited foraging (Eq. (12)).

As depth increases, $\alpha(Z, t)$ decreases as the relative efficiency of visual predation decreases until it approaches zero at depths where visual predation is negligible. In the basic run (the middle curve in plots of Fig. 1), equilibrium depth is reached at about 69 m. Increased light attenuation clearly favours tactile planktivores by reducing the water volume of visual predation superiority. On the other hand the increased size of prey organisms, inherent contrast of prey and surface light favours visual planktivores, the effect being far greater for prey size than inherent contrast, and smallest for changes in surface light. In model runs increased

Table 3
The effects on the equilibrium depth, of 50% decrease and 100% increase in environmental parameters

Parameter:	Variation from the basic run	
	–50% (m)	+100% (m)
Prey abundance (P)	69.0	69.0
Turbidity (K and c)	138.1	34.5
Prey size (β)	55.2	82.9
Inherent contrast of prey (C_0)	62.1	76.0
Surface light (E_0)	62.3	75.9
Turbulence (w^2)	71.1	67.3

Basic run equilibrium depth (= 69.0 m).

prey abundance or turbulence can result in superiority for tactile planktivores throughout the water column (Fig. 1).

Changes in light attenuation has by far the strongest effect on equilibrium depth (Table 3). When measured by equilibrium depth, a reduction in light attenuation of 50% is three times more beneficial for fishes than a doubling of prey size and six times more than a doubling in prey contrast or surface light. Variations in turbulence and prey abundance have only minor effects on the equilibrium depth.

The sensitivity analysis (Table 4) indicate that light attenuation is of greatest importance for both competition measurements ($\alpha(Z, t)$ and Z_{EQ}). While prey abundance and turbulence are of great importance for the competition coefficient they are, however of no (or only little)

Table 4
Sensitivity (S_x) of $\alpha(Z, t)$ and Z_{EQ} to changes in environmental parameters as described in Table 2

Environmental parameter	State variable	
	$\alpha(Z, t)$	Z_{EQ}
Turbidity (K)	–1.07	–1.07
Prey abundance (P)	–0.93	0.00
Turbulence (w^2)	–0.44	–0.04
Prey size (β)	0.24	0.29
Inherent contrast of prey (C_0)	0.12	0.15
Light level at sea surface (E_0)	0.12	0.14

The sensitivity index is given in Eq. (17).

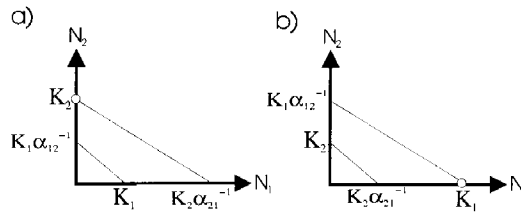


Fig. 2. Zero isoclines for tactile and visual planktivore populations from the basic run. a, The upper parts of the water column where competition among visual planktivores are stronger than competition from tactile planktivores. b, The lower parts of the water column where competition among tactile planktivores are stronger than competition from visual planktivores. (N is population size, K_C is carrying capacity, α is Lotka-Volterra competition coefficients, open circles are stable equilibrium population sizes and the subscripts 1 and 2 denote tactile and visual planktivores respectively.)

importance for location of the equilibrium depth. Prey size, inherent contrast of prey and light level at the sea surface are about equally important to both measurements.

Zero isoclines for changes in both planktivore populations may be calculated from Eqs. (1a) and (1b) by denoting the tactile and visual planktivore populations 1 and 2 respectively. From basic run competition coefficients it follows that the visual planktivore population should dominate at shallow depths (Fig. 2a). Higher in the water column the difference between zero isoclines of the two planktivore populations should be equal to Fig. 2a or even more in favor of the visual planktivores. Likewise at greater depths, tactile planktivores are expected to be competitively superior (Fig. 2b), and zero isocline differences for greater depths might be equal to this or even more in favor of these organisms. The volume of water between the two regions of Fig. 2. will contain the equilibrium depth where the two planktivores are equally effective, thus competition between tactile and visual planktivores are equally strong for both, and the zero isoclines for both planktivores will overlap.

Simulations of habitat profitability under influence of predation shows that both the visual and the tactile planktivores are capable of positive growth rates in near surface waters at night (Fig. 3). While this is partly due to the high prey abundance in shallow waters the main reason lies

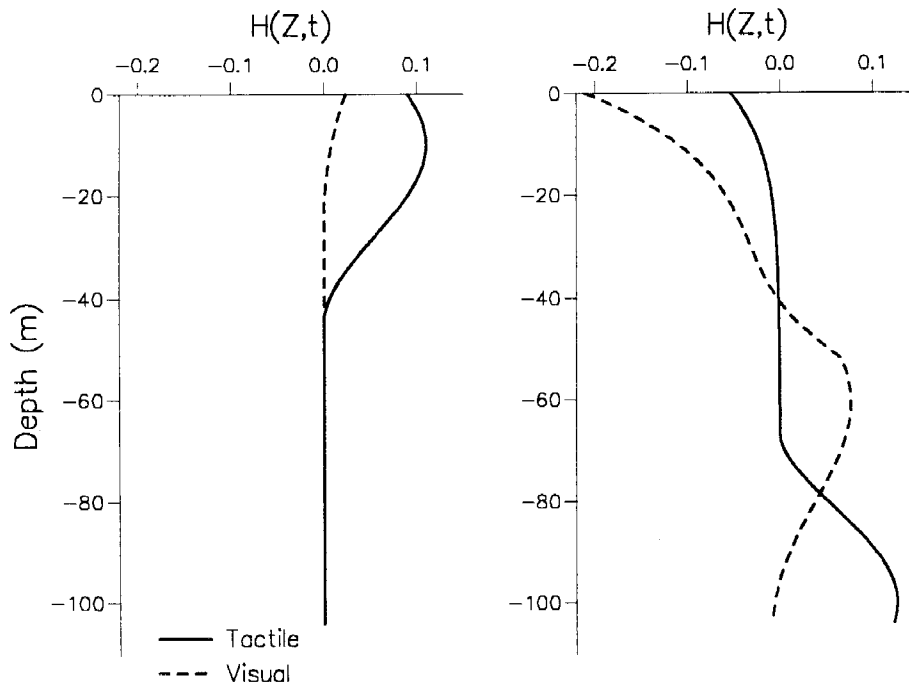


Fig. 3. Depth specific habitat profitability ($H = dN dt^{-1}$), as gC/m, for visual (broken lines) and tactile (solid lines) planktivore populations under predation from a higher order (visual) predator. a, Shows a night situation and b, is a day situation (both of 12 h duration). Prey organisms show a diel vertical migration behaviour. The day situation is represented by abundant surface light and prey maximum (ca. 1000 ind/m) located deep in the water column (100 m), while the night situation is represented by poor surface light conditions and a prey maximum located near the surface (10 m). See Table 2 for a list of parameter values used in simulations.

in the weak predation pressure associated with the low light intensities. In the day situation however, the pressure from the higher order predator results in a net loss for both tactile and visual planktivores in near surface waters. Under such circumstances the visual planktivore population is only capable of an increment at some intermediate depths. In the present simulation this happens from about 40 to about 100 m. The tactile planktivore is only capable of positive growth below a certain depth. In the simulation shown in Fig. 3 this happens below about 70 m.

4. Discussion

4.1. The competitive regime

If the total water column is viewed as the fundamental niche, separate regions for which

the distinctions in Fig. 2 hold denote the realizable niches for visual and tactile planktivores in terms of a one dimensional (depth) niche (Hutchinson, 1957). Notice that the niche concept used here deals with functional groups of planktivores and not with species as did Hutchinson (1957). Following Gause's principle visual planktivores should be present in the upper regions only and tactile planktivores in the lower regions only. Furthermore, no co-occurrence should take place. This of course is not common in nature but is a model artifact caused by the static properties of the basic run. As will be shown below, the inclusion of predation upon the competitors modifies this picture. Nevertheless, basic run results show that based on exploitative competition for a common food resource, the water column is divided into regions of different profitability for tactile and visual planktivores.

Alternations in the environment affects the competition parameters thereby bringing about changes in the zero isoclines shown in Fig. 2. Several of these environmental changes might occur constantly over time. For instance the light regime is constantly changing, due to daily, seasonal, meteorological and biological variations. As shown above, at some 'theoretical depth' in the water column, zero isoclines computed from exploitative competition, for one resource only, will overlap. At the immediate surrounding depths zero isoclines will be almost parallel and close to each other. In this region environmental changes might alter orientations of the two isoclines, thereby changing the nature of the population equilibrium. Further away from the equilibrium depth the distance between isoclines increases and stronger environmental impact is needed (therefore the probability decreases) for shifts in the system equilibrium. Therefore there exists a water volume of instability in respect to the equilibrium population size between the regions of constant superiority. This water volume can be thought of as an ecotone of a rather unpredictable, ever changing, competitive regime.

4.2. Spatial and temporal variations

If one considers the effect on zero isoclines throughout the water column, or the equilibrium depth, water optics is of greatest importance. Attenuation of light in water is dependent on dissolved and particulate matter and therefore a factor that, together with prey abundance, is likely to differ much over time and space. Our results show that the relatively clear waters and low zooplankton abundance of open oceans (Ryther, 1969) provides a competitive regime in favor of visual planktivores. Coastal waters, of higher light attenuation and prey production, on the other hand provides a competitive regime favoring tactile planktivores. Large abundances of common gelatinous zooplankton species are found almost exclusively in coastal waters (Möller, 1980b; Alldredge, 1984).

The static properties of the model predicts only small competitive effects from changes in surface light of the magnitude associated with varying

cloud cover (Fig. 1). However, variations in solar angles over the day and the season undoubtedly effects the equilibrium depth and zero isoclines throughout the water column. Variations in light regime over the day has proved of significance for the habitat profitability of planktivore organisms (Rosland and Giske, 1994). Changes in habitat volume are believed to be largest during winter (except for ice covered areas) and in open oceans due to the clearer waters under these regimes.

Temperate waters undergo strong seasonal changes in water quality. Local chlorophyll *a* concentrations in Norwegian fjords, changes from about 0.03–0.20 (mg/m³) in winter (Noji et al., 1993) to a maximum at spring bloom peak of more than 12.0 (mg/m³) (Skjoldal and Lännergren, 1978). According to the relationship provided by Riley (1956) this gives a seasonal change in diffuse light attenuation coefficients from 0.045 to 0.43/m or about an order of magnitude. Our results conclude such an increase in light attenuation significantly changes the competitive regime of the water column in favor of tactile planktivores (Fig. 1 and Table 3).

The clear waters and low zooplankton abundances in winter provides a competitive regime in favor of visual planktivores (Fig. 1). In nature some of the commonest gelatinous zooplankton (such as *A. aurita*) are virtually absent from the water column during winter (Möller, 1979; Brewer, 1989). Spring successions and its effects on the water column properties, change the competitive regime in favor of tactile planktivores (Fig. 1). It is after the onset of the spring bloom that most medusa and ctenophores becomes dominant members of the pelagic ecosystem in temperate coastal waters (Möller, 1979, 1980b, 1984; Brewer, 1989). The less pronounced spring bloom of subtropical and tropical waters does not provide such temporal favorable conditions for tactile planktivores. In the Mediterranean for instance medusa are present throughout most of the year (Rottini Sandrini and Avian, 1991), but see Axiak et al. (1991).

At high prey abundances the present work concludes that tactile planktivores are capable of higher growth rates than visual planktivores throughout the water column since gelatinous or-

ganisms are capable of linear functional responses and tremendous developmental and numerical response to increases in prey abundance (Alldredge, 1984; Kremer and Reeve, 1989). This effect is dynamic since high abundance of tactile planktivores are known to regulate their prey (Reeve and Walters, 1978; Deason and Smayda, 1982). Our results suggest the increasing carrying capacities and turbidity associated with spring blooms might result in (a temporary) competitive regime favoring the tactile planktivores.

4.3. Eutrophication and alternations in food webs

Fresh water runoff increases light attenuation directly (Cyrus and Blaber, 1992), and through increased phytoplankton production (Ryther and Dunstan, 1971). Zaitsev (1992) claims this to be responsible for the decimation of benthic algae in the Black Sea, but does not link the tremendous increase in gelatinous zooplankton and decrease in commercially harvested fish species with this. Since our results show that the competitive regime is extremely sensitive to light attenuation (Fig. 1), we suggest the changed optical regime of the Black Sea (as described by Zaitsev (1992)) are of vital importance for the change in type of dominating planktivores.

Greve and Parsons (1977) claim tritrophic relations of importance in shaping planktonic food webs. They make a distinction between systems dominated by small primary producers (flagellates) and large primary producers (diatoms). The former system they argue is dominated by small grazers and favors coelenterates as top predators, while in the latter system larger grazers predominate and fish dominate as top predators. Similar arguments have been put forth to describe of the evolution of planktonic predation types, and the food chain difference between upwelling and convergent ecosystems (Parsons, 1979). The (large) diatoms have proven more sensitive to pollution (from hydrocarbons) than flagellates, resulting in nanoplankton dominance, and possibly tactile top predators, under such conditions (Dunstan et al., 1975; Greve and Parsons, 1977). Furthermore Zaitsev (1992) links the eutrophication and pollution of the Black

Sea to a shift towards smaller zooplankton and *A. aurita* and *M. leidy* as dominating top predators. This effect of altered prey sizes is indeed reflected in the present work, however, our model predicts water optics to be of even greater importance for competition (Eqs. (8) and (9)), indicating the latter factor is of chief importance in structuring food webs whenever eutrophication occurs.

4.4. Meteorological variations

Meteorological factors such as temperature, rainfall and wind affects competition. Seasonal differences in fresh water input from rivers depend on snow melting or rain fall. Aarthun (1961) claims the particle content in melting water affects the turbidity regime of a Norwegian fjord system. Similarly, Cyrus and Blaber (1992) show high turbidity as a result of increased river flow in the rainy periods in Australia. Furthermore, mass appearances of *P. noctiluca* in the western Mediterranean Sea appear to be predictable from climatic variables such as temperature, atmospheric pressure and rainfall (Goy et al., 1989). The three factors are clearly related, and an effect on near shore waters is to increase light attenuation, as shown above.

During rainy periods the amount of incoming light is reduced, by up to as much as 80% from that of clear sky values (Sathyendranath and Platt, 1989). While similar variations in the surface light only slightly affects competition (Fig. 1 and Table 3), this nevertheless adds to a competitive regime favoring tactile planktivores.

Sundby and Fossum (1990) showed the importance of wind induced turbulence for the encounter rates between larval cod and its prey, and hence the survival of cod. In our work, the tactile planktivore profits most from turbulence due to slower swimming speeds than visual planktivores. The main source for small scale turbulence, tides and winds, has most pronounced effects on surface near water, thus mixing depths typically are confined to the upper parts of the water column. It is often within these depths that prey are likely to be encountered in largest numbers in nature. For highly

turbulent waters, the model actually predicts tactile planktivores capable of the highest prey removal rates virtually throughout the water column (Fig. 1), even at midday.

4.5. Predation

The general conclusion that arises from the competitive interactions is that tactile planktivores are better off if they stay at greater depths than visual predators (which are best off if they stay near the surface). However, risk of predation might not allow the visual planktivores to maintain its populations at shallow depths (Fig. 3). If visual planktivores tend to avoid surface waters, competition here will decrease or disappear for the tactile planktivore. This might result in tactile planktivores being present both at shallow and greater depths, while visual predators are confined to an intermediate part of the water column, balancing predation risk and foraging efficiency (or competition). Such a strategy has been shown to be optimal for *M. muelleri* (Rosland and Giske, 1994; Giske and Salvanes, 1995).

The high transparency of gelatinous zooplankton combined with high turbidity in highly illuminated surroundings greatly reduce the inherent contrast of these creatures and thus their encounter risk with visual planktivores (Chapman, 1976; Giske et al., 1994). On the other hand, gelatinous zooplankton are not capable of the swift escape responses fish show to approaching predators, and presumably they are much poorer at the detection of an approaching danger. Consequently, gelatinous zooplankton might represent prey of higher vulnerability to organisms of higher trophic levels. Yet, the low food quality of most tactile planktivores adds to the presumption that under high predation pressure, or under strong influence of commercial fisheries (Parsons, 1992) tactile planktivores might improve their competitive relations indirectly by decreased mortality relative to their competitors. In addition to this effect, predation pressure might also affect the relative competitive abilities of organisms (Abrahams, 1994).

4.6. Complications

Model calculations are made on immediate time scales for individual organisms. The outcome of exploitative competition is also dependent on the size of competing populations, carrying capacity of the habitat, life history traits of the organisms involved, and the time span over which the conflicts occur (Begon et al., 1990). Unfortunately, these problems can not easily be solved due to lack of knowledge on the life history and physiological traits of the organisms in question. Furthermore, in this work, competition is studied under a high noon situation. This yields a maximum benefit for visual planktivores. Most of the time however, the environment is less favorable for visual planktivores, resulting in a narrower niche for these competitors.

There are no direct ways in which the 'real profitability' of a sub habitat can be extracted from $\alpha(Z, t)$ and Z_{EQ} since they only deal with potential foraging rates. In nature several other factors such as predation (Möller, 1980b) and density independent factors (e.g. temperature (Legovic, 1987)), might be of even greater importance in determining the fitness of planktonic organisms. Such factors have been shown to affect the organisms' fitness (Aksnes and Giske, 1990), its habitat preference and are suggested driving forces of vertical migrations (McLaren, 1963; Boden and Kampa, 1967; Blaxter, 1986; Iwasa, 1982).

While adult fish and jellyfish compete by functionally different exploitation of a common food resource, other interactions such as competition by inference might prove of greater importance over the organism's total life span. Adult jellyfish are known to be voracious predators on fish larvae (Bailey and Batty, 1983; Arai, 1991), and Möller (1984) shows that large *A. aurita* populations may regulate herring production in the Baltic Sea both through competition and predation on larval fish. Little is known of the extent fish prey upon gelatinous zooplankton. The low food quality of these organisms may suggest that they play a minor role in the transfer of energy to higher levels in the food web. Nevertheless, fish preying on jellyfish are known from the literature

(Fraser, 1970). When competitors prey on their counterparts offspring, competition for food might be of less importance in shaping planktonic communities.

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